

NESTING SUCCESS CALCULATED FROM EXPOSURE

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IN reporting the nesting success of birds, it is customary to give the numbers of nests and eggs in the sample, the number of eggs that hatch, the number of young birds fledged, and various percentages derived from these.

In my analysis of the nesting success of the Kirtland's Warbler (*Dendroica kirtlandii*) I had shortcomings and subtleties in my data that could not be treated satisfactorily by the customary methods. Most serious of these problems was the fact that many of the nests in my sample had not been found until after incubation had begun. That others did not mention such difficulties was not reassuring but rather aroused the suspicion that some of their findings might not be so exact as the cold finality of their figures seemed to imply.

Consequently, I proposed a new way of analyzing data of this kind (Mayfield, 1960. *The Kirtland's Warbler*. Cranbrook Inst. of Sci., Bloomfield Hills, pp. 182-209). There, however, the method was incidental to the results, and it was complicated at every turn by the effect of Brown-headed Cowbirds (*Molothrus ater*) in the nests with the warblers. So I am offering here a simplified explanation for the benefit of field workers with little training in mathematics.

DIFFICULTIES WITH CUSTOMARY METHODS

In studying the nesting success of birds, we want to know how many of the nests *built* produce fledglings and how many of the eggs *laid* hatch and ultimately become fledglings. In fact, these are the terms customarily used in presenting the results of field work. But I believe that these results are often misleading, because the production is actually calculated from nests and eggs *found*—not the same thing as nests *built* and eggs *laid*.

To illustrate, suppose we were to find a series of nests on the eve of hatching. In this special group the "hatching success" would be nearly 100 per cent, and subsequently the "nest success" and "success of eggs to fledging" would be almost twice as high as if these nests had been discovered at the start of incubation. No such extreme example is likely to occur in field work, but the problem exists to a variable and unknown extent in nearly all studies of birds with concealed nests. Only among birds whose nest sites are under observation before the birds use them, such as those using artificial cavities, are all the records likely to be complete from the very beginning.

Of course, if all nests were discovered with the first wisp of building material and followed through to termination, analysis would present few difficulties and this discussion would be unnecessary. In truth, however, the raw data are not likely to be as tidy as the published summaries would seem to indicate. With open-nesting altricial birds, typically, the field worker finds a few nests

during the building stage, a very few during the egg-laying stage, a larger number during the incubation stage, and perhaps the greatest number during the nestling stage. Thus, his records include nests found at every way station of development, and these are somehow lumped together to calculate "success," expressed perhaps as percentages of nests *built* and eggs *laid* although few of the nests were found when just built or when the eggs were just laid.

How serious an error this may be can be seen in another hypothetical example, a little more realistic than the previous one but still simplified enough for easy comprehension without mathematics. Suppose we were to find an equal number of eggs on each day of the incubation period. It is intuitively obvious that the losses observed up to hatching time will be only about half what they would have been if we had found each nest at the start of incubation. That is, many of these nests were well on their way to success when found, or, saying it another way, a good many unsuccessful nests were lost before we got there and thus escaped our attention. Now suppose this series yields a fairly typical apparent "hatching success" of 60 per cent of eggs *found*, or a mortality of 40 per cent of eggs *found*. But, egg mortality occurs mostly through destruction and desertion of entire nests, and we have recognized that nest losses are not adequately represented in our sample. Consequently, the true "success" of the species is very much lower than the apparent success we have calculated from nests found. Similarly, we may wonder if the true success of many open-nesting species is less than the published percentages.

In some studies the discrepancies may not be so great as those in my hypothetical examples, because life-history workers often make a special effort to find nests early. But how can we be sure? Are these factors consistent from one study to another? In one species it may be harder to find nests early than in another. One observer may not be on the nesting ground as early in the season as another. It is unsettling to think that nesting success and mortality reported in studies may be in part an artifact of nest-finding practices.

Indeed, a mortality or survival rate has meaning only if a period of *time* is specified; and, if the period is not stated in units of time, the rate will be assumed to apply to the entire stage of existence under consideration. That is, a mortality or survival rate given for the incubation period is presumed to be based on observation from the very start of incubation.

Yet, if observers throw out all records except those on nests found before the start of incubation, their study samples are likely to become very small (at a serious cost in reliability), and also much useful information may be discarded.

This brings us to another subtlety in quantifying our nesting data. Sometimes observers are unable to follow every nest through to a conclusion and

so have fragments of information on nests whose outcomes are unknown. What should they do with these fragments? Cautious individuals may exclude these from their calculations. Yet, to do so, inflates the mortality rates; that is, a nest destroyed quickly is likely to be included because its fate is known, while a nest that endures until after the observer has departed is likely to be disqualified because its outcome is unknown. On the other hand, other individuals, eager to report as many nests as possible, may include these nests, enlarging the sample without enlarging the losses. To do so, understates the mortality. Here is an awkward dilemma: either to include or to exclude nests with outcome unknown threatens to distort the results.

NEST-DAY AS A UNIT OF EXPOSURE

There is a way out of these difficulties. Briefly, it recognizes that the number of nests lost will vary with the number of nests and also with the time span covered by the observations. The combination of these two—nests and time—I call exposure.

A convenient unit of exposure is the nest-day; that is, one nest for one day. Thus, a nest under observation for ten days represents an exposure of ten nest-days, which is equivalent to the exposure of ten nests for one day each, or five nests for two days each, or any combination of nests and days whose product is ten. Thus, the total exposure of a group of nests is the summation of all the days spanned by observation at each nest. (For some calculations greater precision may be offered by a smaller unit, the egg-day; but, for simplicity, I will restrict myself chiefly to the nest-day in this discussion.)

Nests seen only once are not counted because they do not span any period of time. A nest seen on two consecutive days represents an exposure of one nest-day. A nest in existence five days after it was found represents an exposure of five nest-days whether it was visited many times or only at the end of that interval. A nest lost during an interval of several days is arbitrarily assumed to have been lost on the day at the middle of the interval. All days spanned by observation are included even though no change occurs.

Now we can utilize fragments of information and combine them into a meaningful whole. We can calculate the probability of survival looking backward or forward in any period for which we have survival rates, just as the insurance actuary predicts survival at any stage of human life. Also we can combine scanty bits of information from different observers, the only kind of information we are likely to have on certain elusive species for a very long time.

NEST MORTALITY DURING INCUBATION

To illustrate this method of analysis, we may consider my data on the Kirtland's Warbler, examining first the incubation period. My data on 154 nests

of the Kirtland's Warbler seen during incubation represent a total exposure of 878 nest-days. It is of interest that 10.3 nest-days is equivalent to the average life of one of these nests during incubation (Mayfield, op. cit.), and therefore if I had been so fortunate as to have had information on all these nests from the very start of incubation up to hatching or termination short of hatching, I would have had nearly twice this exposure. It is worth noting also that if I had included only nests with outcome known, I would have been able to use information from only 113 instead of 154 nests.

In this sample I recorded 35 nests lost (19 destroyed and 16 deserted) in 878 nest-days exposure during incubation. So the mortality rate is $35 / 878 = .040$ nests lost per nest-day during incubation.

Now, knowing the attrition per nest-day, we can calculate the losses back to the start of incubation even though not many of our nests were observed from the very start. In fact, we can take a sample at any point and calculate the probable number in existence on any earlier or later day within the incubation period.

For example, suppose we have 100 Kirtland's Warbler nests incubating. By tomorrow, we can expect to lose four of these nests; by the following day, 4 per cent of the remainder; and on any succeeding day, 4 per cent of the previous day's remainder. Thus, at first we lose almost four nests each day, but as the sample shrinks, so do the losses. When only 75 nests are left, the losses shrink to three a day. It is like compound interest in reverse; the principal shrinks while the rate remains the same.

Here we assume that the hazards of existence are constant throughout the incubation period. Inspection of my data suggests that this is at least approximately true, although I do not have a sufficiently large number of early and late losses to prove conclusively that they are as likely to occur in one part of incubation as another. This assumption is supported also by the fact that I have been unable to detect any change in the behavior of the bird that would appear to increase the vulnerability of the nest early or late in the incubation period. (If this assumption should need modification in some species—for example, if losses are greater early in incubation—this fact will send even farther astray the customary method of ignoring losses before nests are found; the greater the early losses, the more the results will be distorted by including nests not found at the very start of incubation.)

NEST SURVIVAL DURING INCUBATION

The *losses* are directly proportional to the exposure; so thus far, I have used only the *mortality* rate. For some calculations, however, it is more convenient to use the converse, the survival rate. For example, suppose we have 100 Kirtland's Warbler nests under incubation; then tomorrow, as shown in the

previous paragraph, we can expect to have 96 of them left; the following day 96 per cent of 96 ($.96^2 \times 100$); and on each following day 96 per cent of the preceding day's remainder ($.96^3 \times 100$, $.96^4 \times 100$, . . . and so on to the end of incubation). Now, in the Kirtland's Warbler, with an average incubation period of 14 days, the probability of survival for the incubation period is $.96^{14} = .56$. That is, 100 nests at the start of incubation would be expected to shrink to 56 nests at hatching time.

Generalizing and expressing the result in better mathematical form, the probability of survival of nests with a mortality rate r for a period of days d is $(1 - r)^d$; or, since $1 - r$ is the survival rate S , the probability of survival is S^d .

NEST SURVIVAL DURING NESTLING PERIOD

When young hatch, of course, the hazards of existence for the nest change abruptly. But we can proceed with our calculations in a similar way, using new mortality and survival rates, as follows: I have records on 144 nests of the Kirtland's Warbler observed during the nestling period, with a total exposure of 735 nest-days. In this group, 22 nests were lost, 19 of them destroyed and 3 deserted. (It is interesting to note that the rate of destruction of nests is virtually unchanged from the incubation period but the rate of desertion is much lower.) So the mortality rate for nests during the nestling period was $22/735 = .030$ nests per day, and conversely, the survival rate was $.97$. Since the young Kirtland's Warbler usually leaves the nest at the age of nine days, the probability of the nest's survival for the nestling period is $.97^9 = .76$.

NEST SURVIVAL FROM START OF INCUBATION TO FLEDGING

These figures drawn from different nest periods and different samples may be combined, through the mathematical principle that the probability of two successive events is the product of their separate probabilities. Hence, the probability that Kirtland's Warbler nests will survive both the incubation and the nestling periods—that is, from the start of incubation to fledging—is $.56 \times .76 = .43$.

EGG SURVIVAL DURING INCUBATION

The Kirtland's Warbler, unmolested by the cowbird, loses very few eggs without loss of the entire nest; so egg survival is virtually equivalent to nest survival during incubation.

To appraise this matter more precisely, it may be calculated from the loss of six individual eggs during an exposure of 3,181 egg-days that the mortality among eggs was .002 eggs per egg-day and that the probability of survival for 14 days was $.998^{14} = .97$. That is, 97 per cent of eggs starting incubation may be expected to be present at hatching time if no nests are lost. Here the loss of individual eggs is so small there is some question if this factor need be

included in the analysis. In small samples the imprecision in basic data may not justify such refinement in computation. But, with other species, losses of this kind may be significant, and, for illustrative purposes, this small shrinkage will be treated here along with the other losses.

Combining the two probabilities just calculated, we have $.56$ (probability of nest survival during incubation) $\times .97$ (probability that eggs will survive individual loss) = $.54$ (probability of egg survival during incubation).

NESTLING SURVIVAL DURING HATCHING PERIOD

Before we can link egg survival during incubation to nestling survival in order to get production of fledglings from eggs that start incubation, we need to know the hatching success of the eggs present at hatching time.

Here again our observations are not likely to be as exact as figures seem to imply. Unless every nest is under constant scrutiny—a rare circumstance—it is impossible to be sure exactly how many eggs hatch. For example, a nest containing five eggs one afternoon may contain one egg and three newly hatched young when visited the next morning. What happened to the missing egg? Are we justified in saying it did not hatch? Perhaps it hatched and then was removed by predator or parent.

The parent Kirtland's Warblers remove dead nestlings and damaged eggs promptly. A young bird that pips its shell but does not emerge fairly soon is in danger of removal, as is an egg with shell pierced by bill or claw. Therefore, I have not attempted to separate hatching success from individual survival in the first few hours of life, but consider these two questions under one heading, survival of the hatching period. For this species, it seemed proper to define the hatching period as the two days following the hatching of the first egg in the same nest. (Some Kirtland's Warbler eggs hatch as much as a day later than others in the same nest but never as much as two days later.)

In my sample, among 182 warbler eggs present at hatching time, in nests without cowbird eggs, 142 nestlings were present two days after the first hatched in each nest. So the probability of survival of the hatching period was $142/182 = .78$.

The probability of survival of individual birds through the hatching event is quite aside from the hazards of existence for each nest as a whole. Therefore, the two days designated as the hatching period must be considered again when we weigh the hazards causing the loss of whole nests (destruction and desertion) rather than the loss of individuals in a nest that survives.

NESTLING SURVIVAL

In the absence of cowbirds, virtually the only losses of individual Kirtland nestlings (without loss of entire nests) occurs in the first day of life. (I have

only one instance of such a nestling lost after the first day and it disappeared on the second day.) Since losses of newly hatched birds were already treated in survival of the hatching period, the probability of survival of nestlings is virtually the same as of nests, which, calculated previously, was .76.

EGG AND NESTLING SURVIVAL FROM START OF INCUBATION TO FLEDGING

Finally, we sum up production for the entire duration of the nest by combining the probabilities for each step, as follows: .54 (probability of egg survival during incubation) \times .78 (probability of nestling survival during the hatching period) \times .76 (probability of nestling survival to fledging) = .32 (probability that eggs at the start of incubation will produce fledglings).

This figure is approximately the production from eggs *laid*; but, to be perfectly precise, we should be aware that up to five days may elapse between the laying of the first egg in a clutch and the start of incubation. Hence, there is some exposure and loss (not treated here) before the start of incubation. In the species used as an example here, I believe this source of shrinkage much less important than those treated in this paper.

SUMMARY

A field worker analyzing data on nest success may be dealing with a sample in which comparatively few nests were found before the start of incubation. Also, his sample may include some nests for which the outcome was unknown. If such partially complete records are included (or excluded) from his calculations, there is danger of distorting the conclusions. "Percentage of nests *found*" is not the same as "percentage of nests *started*" unless every nest was observed from the very start.

One way of dealing with this problem is to reduce the data to units of *exposure*, which reflects not only the number of nests but also the length of time each was under observation. A convenient measure of exposure is the nest-day (equivalent to one nest for one day). With this approach, all observations covering one or more days each can be incorporated into the sample, even though some of these do not go back to the very beginning and do not carry through to the end. By this method, small fragments of information can be combined into a coherent whole. This may be the only kind of information available for a very long time on many elusive species.

After mortality and survival rates are expressed per nest-day, the probability of survival may be calculated for all or any part of the nesting period. If the survival rate per nest-day is S , the probability of survival of a nest for d days is S^d . The rate during incubation is different from the rate during the nestling period, so these two stages must be treated separately. Also, egg survival must be considered separately from nest survival because of the loss of individual eggs, particularly at hatching time. The probabilities of survival in different stages of nesting may be combined through the mathematical principle that the probability of a succession of events is the product of their separate probabilities.

Each step in these calculations is illustrated with facts from my previously published study of the Kirtland's Warbler, with calculations simplified by considering only those nests in the larger study that were not parasitized by cowbirds.

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